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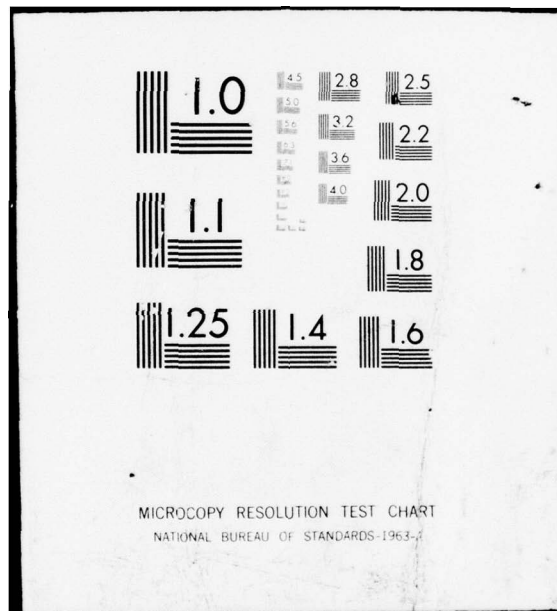
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COMMUNICATION IN SIRENIENS, SEA OTTERS, AND PINNIPEDS,

Howard E. Winn Jack/Schneider

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Introduction

The three groups of marine mammals discussed in this chapter are the Sirenia, the Pinnipedia, and one mustelid,¹ the sea otter (*Enhydra lutris*). The Sirenia are coastal marine, estuarine, and river animals, whereas the sea otter is coastal. In general, the groups have retained their own characteristic modes of communication with little convergence. Their communication is limited and fashioned by the physical and biological characteristics of the environment. These families communicate in water and in air, and the effects of the media on communication must be known to understand signal adaptation.

Visual and acoustic communication are important in both media, depending on the amount of ambient interference. The greatest noises encountered by these marine mammals are surf noise and particulate turbidity (both biological and physical), which are found near the land-water boundary. This interference does not affect all the families equally since in general their habitat selection is varied; however, the otarids and the phocids inhabit similar areas. Northern species contend with less turbidity and, during much of the year, with less biological noise

(i.e., snapping shrimp). Pagophilic species live with optimal visual and acoustic conditions during much of the year, except during plankton blooms and the semiannual absence of sunlight. Except for the extinct family Hydromalidae, the species of Sirenia live in tropical estuaries and rivers with constant high particulate densities and rather low noise levels. The Hydromalidae lived in kelp beds near the margins of subarctic islands, a habitat where good vision and hearing could be adaptive. The sea otter lives in an environment similar to that reported for Hydromalidae, and also along the coast from the Kuril and Aleutian islands to southern California (Kenyon, 1969), with similar environmental demands of good vision and hearing.

The use of olfaction in water may be ruled out because of the slow rate of molecular diffusion in the medium plus the necessity of closing the nares under water. However, both pinnipeds and (only briefly) the sea otter haul out on land, where olfaction could be used, though phylogeny and behavioral need would also be determining factors. Gustatory and tactile signals depend on contact transmission and could be of use in either medium.

The general behavior of sea cows and sea otters in relation to communication will be de-

1. A second marine otter (*Lontra felina*) lives in the coastal waters of Peru and Chile.

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scribed separately, followed by a more in-depth discussion of signaling by pinnipeds. As there have been few natural experimental studies, the function of signals and the relative strength of the communicative channels must be assumed from correlations of signal and behavior.

Sirenia and Sea Otter

SIRENIA

Sirenia are unaggressive grazers that inhabit slow-moving, silty, eutrophic, fresh and marine coastal waters of tropical and subtropical areas (Bertram, 1964; Moore, 1956). They are normally dispersed individually or in small groups, except during mating and cold spells (Moore, 1956). They are totally aquatic, and during normal activity only the dorsally located nostrils (during breathing) and the arch of the back break the surface (Bertram, 1964). Under these conditions, we would expect vision to be less useful than in other environments. Bertram (1964) and True (1884) suggested that vision is poor, though Bertram mentioned that manatees sometimes lift the head quite high out of the water near the bank, perhaps to see.

The importance of the acoustic and tactile senses is stressed in general descriptions of sirenian behavior. Gohar (1957) described the hairs of *Dugong dugong* as being most numerous around the mouthparts, the chin, the muzzle, and the dorsal tail ridge. The bristles around the mouthparts are oriented proximally and may serve to direct food into the mouth. He did not speculate on a function for the trunk hairs. Murie (True, 1884) described manatee feeding: "occasionally it would sniff or examine [various vegetables] by snout and lips without chewing or swallowing. . . ." Descriptions of greeting, play, and mating include accounts of tactile communication, presumably involving the vibrissae.

Mother-young interactions include the mother's supporting the young on her back as she

rests and, occasionally, as she moves. This behavior may be important as a survival mechanism and may also be important in socialization, for it occurs during adult play behavior as well, when nuzzling and body contact result from an animal's rising in the water column, colliding with and raising a second animal (Moore, 1956).

The most complete descriptions of presumed manatee courtship are described by Moore (1956) and confirmed by Caldwell and Caldwell (1972a) as occurring during social aggregations. These authors reported that courtship is a stereotyped progression of tactile interaction.

An animal nuzzled the other animal's side, put its flipper on the other's back, then rolled until its venter was towards the object of its intentions. For once no avoidance move was made by the animal being approached. After a pause the aggressor rolled gently venter down and let his flipper slide off into the water. Paddling softly with his flippers, he explored with his muzzle along the other manatee's side until at about its midlength, during which time his own body had moved away from the other's to a right angle so that the other's long axis crossed his own like the top of a "T." The male then rolled over on its own long axis until venter up (thus revealing his sex) and in this position carried his nuzzling down the other's side to under its belly and explored with his muzzle along towards its genital area. [Moore, 1956]

Copulation was not observed. The use of the foreflipper in maintaining body contact is similar to behavior observed in mating pinnipeds.

Moore (1956) termed muzzle-to-muzzle contact between animals as "greeting." This stereotyped behavior is accompanied by the animals' rising in the water column and maintaining contact with their muzzles above the water surface. Moore speculated that if airborne scent is important in this ritual, it is extremely interesting to find this in-air gesture retained in this former terrestrial animal. He hypothesized that this ceremony facilitates individual recognition. It seems analogous to pinniped behavior, and would seem to be useful to these normally

nonaggressive inhabitants of cloudy water. Manatee breath is said to be sulfurous (Parker, 1922).

Results of behavior studies and acoustic monitoring of manatees suggest the importance of acoustic communication and environmental sensing, although very little is known. Bertram (1964) stated that tame manatees are attracted through conditioning by the human whistle more readily than by other signals; wild manatees are alarmed by the human voice and startled by unusual noises (Barrett, 1935). In their normally quiet, opaque, natural habitat, hearing would be a selectively advantageous channel of communication. Knowing the habits of the manatee, we would expect it to communicate vocally. In a list of the sounds of various mammals, Tembrock (1963) stated that *Trichechus manatus* produces a 4,304 Hz call. This result is similar to those of the more comprehensive study by Schevill and Watkins (1965), who found that the fundamental tones of *T. manatus* vocalizations are at 2.5 to 5 kHz, but may be as low as 600 Hz. They described the calls as squeaky and rather ragged, and stated that they lasted 0.15 to 0.5 sec and were 10–12 db above background at distances of 3 to 4 m. Evans and Herald (1970) reported similar results from their studies of *T. inunguis*. The major differences between the calls of the two species appear to be the fundamental frequency, which is 6 to 8 kHz for *T. inunguis* as compared to 2.5 to 5 kHz for the Florida species, and the occurrence of pulses associated with some calls produced by the Amazon species. These observations were made in captivity, and no evidence was given for the function of the calls.

Hartman (1969) reported that the underwater sounds of the manatee are highly variable and include chirp-squeaks, squeals, and screams, all produced in a variety of unrelated circumstances. They seem to be associated with emotional states, especially alarm, and are not used in echolocation. One predictable vocal reaction is the alarm duet between a mother and her calf as she calls it to her side before fleeing (Hart-

man, 1969). It should be noted that when startled, the manatee will plunge into the water using the force of its tail and create great turbulence and noise, which may have communicative function (True, 1884). Krumholz (1943) described the behavior of a startled group in which the male reared out of the water and headed with two females for deeper water, while another female and a pup fled in the opposite direction. Arthur Myrberg (pers. comm.), in a recent study of sounds made by a male, a mother, and a baby, heard sounds from each individual, and the vocabulary seemed limited. Manatee sounds are much like gull shrieks, and are produced in social interactions. The baby made quite a few sounds when isolated.

SEA OTTER

In Alaska, the mature sea otter is normally solitary or found in small groups (Kenyon, 1969, 1972). In California, Fisher (1939) observed groups of sixty to eighty. The otter is rarely found on land, except when nursing, pupping, or resting (Kenyon, 1969; Barabash-Nikiforov, 1947). Sandegren et al. (1973) never observed the otter on land in California, though Vandever (1971) did.

The sea otter spends the majority of its life in the water, swimming, grooming, feeding, and mating (Kenyon, 1969). The animals may habitually frequent the same areas to feed (Limbaugh, 1961; Fisher, 1940). There is evidence that male sea otters breeding in Alaska do not hold aquatic or terrestrial territories (Kenyon, 1969), although aquatic territoriality has been observed in the sea otter in California (Vandever, 1970), and Fisher's (1939) observations imply a dominance hierarchy in the California sea otter. Recently, Calkins and Lent (1975) have observed territoriality in some Alaskan sea otters; its expression may be related to topographic factors. These authors describe the male patrolling his territory and chasing intruders, and an occa-

sional fight. Autogrooming by the defending male typically followed a chase. The male patrolled on his back, vigorously kicking and splashing, thus providing a highly audible and visible display. The absence of rigid aquatic territoriality may account for the lack of anal scent glands, which are found in other mustelids (Kenyon, 1969).

Smell is important for environmental sensing and for intraspecific communication in air, but it may not be used under water. In an early evaluation of sea otter senses, Elliot (1887) wrote:

The quick hearing and the acute smell possessed by the sea otter are not surpassed by any other creatures known to sea or land. They will take alarm and leave from the effects of a small fire as far as 4 or 5 miles to the windward of them, and the footsteps of a man must be washed by many an ebb and flood before its traces upon the beach cease to alarm this animal and drive it from landing there, should it happen to approach for that purpose.

Barabash-Nikiforov (1935) observed that the sea otter bed is located in the shelter of some spur or projecting rock, and the direction of the exit tracks seems to indicate that the animal lies with its head pointing up wind. By Kenyon's (1969) account, smell may function in individual recognition or to indicate estrus. He observed a precopulatory male searching for the female by sniffing. During courtship the male will monitor the air at the water's surface and will change direction as much as 130° when arriving downwind from a feeding female (Vandever, 1970). This is accompanied by anogenital inspection of animals by mature males (Fisher, 1939; Kenyon, 1969; Vandever, 1970), which suggests pheromone secretion. In this behavior, the male cruises among the raft of animals, inspecting each one until his advances evoke a response that leads to mating.

During courtship, the male seems to propel the female by pushing with his nose against her anogenital region (Vandever, 1970); he possi-

bly receives an olfactory cue from this action, and he may be stimulated by vision and taste. Kenyon (1969) suggested that sea otters can distinguish food items by taste, and it would seem likely that estrus would be accompanied by a combination of cues including taste, odor, and vision, as in other mammals.

Kenyon (1969) and Fisher (1939) reported that mating behavior includes the male's positioning himself on top and biting the female's head region; in pinnipeds, this causes the female to become rigid (Kenyon, 1969) or limp (Vandever, 1970), depending on the population of animals. Intromission follows. Should the male lose his grip, it must be reestablished for female acceptance. It would seem probable that this action arises ontogenetically from infancy, for the female carries her pup on land by biting its head (Kenyon, 1969).

Sea otter communication is dominated by hearing, vision, and touch. Tactile communication involves licking; contact with general body surface, forepaws, and vibrissa; and copulation.

Licking has been observed in maternal grooming of the young's pelage and anogenital region, where it probably stimulates defecation and prevents soiling of the fur of the mother and the young (Sandegren et al., 1973). This behavior may have an important function in communication, not only in signaling estrus but also in maintaining the mother-young bond and in providing comfort to the distressed young. Licking the head in a stereotyped manner seems to bear no relation to cleanliness or hunger and appears to comfort the pup in a stressful situation (Sandegren et al., 1973). Body contact and contact maintained by the forepaws may also serve the same ends (Fisher, 1940; Kenyon, 1969; Sandegren et al., 1973), as pups crying in distress cease calling when contact with the mother is made.

The adults' ability to find and identify food depends on tactile identification of food objects

at the depths where food is found (Kenyon, 1969; Sandegren et al., 1973). Food is also identified by vibrissa contact; Kenyon (1969) stated that the vibrissae are abraded off in wild, foraging adults but not in captive animals. In Kenyon's (1969) photograph of a sea otter being offered food, the vibrissae are extended forward and are apparently touching the food object, in a manner identical to the vibrissa action in feeding seals. The vibrissae are voluntarily controlled, and when extended forward they serve as a sensory aid when the otter is walking among rocks or examining a strange object (Kenyon, 1969). The use of vibrissae in individual recognition or in sexual-agonistic signaling is postulated.

In some circumstances vision seems less important to the sea otter than hearing or olfaction (Kenyon, 1969), although obviously these animals have good vision, which is continually used in communication. Certain postures convey alarm and warning. When alarmed, the sea otter will rise halfway out of the water (Scammon, 1874; Kenyon, 1969; Vandever, 1970; Fisher, 1939). Whether this maneuver merely affords the animal a visual vantage or whether it contains message value for other sea otters is not known, but it is an oft-observed and stereotyped action.

Mating animals have been observed to swim in coordination, the male following the dives and surfacing pattern of the female (Kenyon, 1969). The importance of this behavior in communication and reproduction is not mentioned, though its stereotyped character would suggest its use in communication.

Though the sea otter lacks piloerector muscles (Kenyon, 1969), it displays a defensive posture similar to that found in other mammalian species. According to Kenyon's (1969) photograph and comment, the threatened animal hunches up, and may hiss and attempt to bite and push the intruder with its paws. The male's mating posture, with feet held high out of the water

(Fisher, 1939), and his red penis are highly visible signals.

Vision is important in maintaining the mother-young bond. The mother watches the pup constantly (Kenyon, 1969), and when the mother and pup are out of sight of each other, both of them will cry until they are in contact (Kenyon, 1969; Sandegren et al., 1973; Fisher, 1939). The pup cry can be heard by humans at such a distance that twelve-power binoculars were not sufficient to locate the pup (Fisher, 1940).

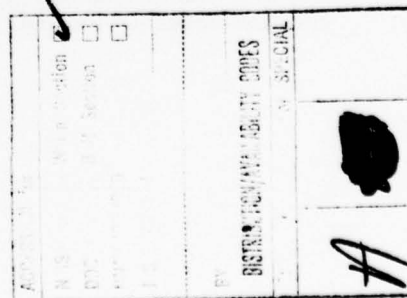
A variety of sounds are made by sea otters (Kenyon, 1969; Fisher, 1940; Sandegren et al., 1973; Limbaugh, 1961; Vandever, 1970), including the baby cry, the adult scream under stress, the adult female scream when separated from her young, the whistle or whine under conditions of frustration or mild distress, the contentment cooing of females during premating and postmating behavior, aggressive snarls or growls when trying to escape, hissing, grunts during feeding, and aggressive or frustration barks.

In summary, the sea otter depends primarily on hearing, olfaction, vision, and touch for communication. Because of the lack of experimental data, we have relied on field observation of social behavior, inasmuch as there is no social behavior without communication.

Pinnipedia

Pinnipeds divide into three families: Otariidae (sea lions and fur seals), Odobenidae (walrus), and Phocidae (northern true seals, antarctic seals, monk seals, hooded seals, and elephant seals). All the otarids and the walrus are polygynous. The phocids have a few polygamous social groups (elephant seals and some populations of grey seals), but most are assumed to be monogamous.

We have used common names for seals as follows: Steller or northern sea lion (*Eumatopias*



jubatus), California sea lion (*Zalophus californianus*), southern sea lion (*Otaria byronia*), Australian sea lion (*Neophoca cinerea*), Hookers sea lion (*Phocarcetos hookeri*), northern fur seal (*Callorhinus ursinus*), South American fur seal (*Arctocephalus australis*), South African fur seal (*A. pusillus*), Kerguelen fur seal (*A. tropicalis*), Guadalupe fur seal (*A. philippii*), Australian fur seal (*A. doriferus*), Tasmanian fur seal (*A. tasmanicus*), New Zealand fur seal (*A. forsteri*), walrus (*Odobenus rosmarus*), bearded seal (*Erignathus barbatus*), grey seal (*Halichoerus grypus*), harbor seal (*Phoca vitulina*), ringed seal (*P. hispida*), Caspian seal (*P. caspia*), Baikal seal (*P. sibirica*), harp seal (*P. groenlandicus*), ribbon seal (*P. fasciata*), Weddell seal (*Leptonychotes weddelli*), crabeater seal (*Lobodon carcinophages*), leopard seal (*Hydrurga leptonyx*), Ross seal (*Ommatophoca rossi*), Mediterranean monk seal (*Monachus monachus*), West Indian monk seal (*M. tropicalis*), Hawaiian monk seal (*M. schauinslandi*), hooded seal (*Cystophora cristata*), southern elephant seal (*Mirounga leonina*), and northern elephant seal (*Mirounga angustirostris*).

The nomenclature is from King (1964), except for uniting the genera *Pusa*, *Pagophilus*, and *Histiophoca* into the genus *Phoca* (Burns and Fay, 1970).

PINNIPED RECEPTORS

Vision

The eye of the seal is well developed (Walls, 1963; Lavigne and Ronald, 1972; Jamieson and Fisher, 1970, 1971; Piggins, 1970; Nagy and Ronald, 1970; Hobson, 1966; Johnson, 1893; Landau and Dawson, 1970; King, 1964; Wilson, 1970). The large spherical lens is adapted to aquatic vision, the refractive index of the cornea being similar to that of water. On land, under lighted conditions, pinniped vision is good. The vertical slitlike pupil adapts the eye to aerial vision by reducing astigmatism, sharpening the focus, and reducing the light. Under low-light

conditions in air, the pupil is dilated and the animals have poor form vision (Schusterman, 1968, 1972; Schusterman and Balliet, 1971). Because of the general absence of land predators, vision need not be too acute at night on land. The predominantly rod-dominated retina and *tapetum lucidum* adapt the eye to the low light levels found in the water. In the harp seal, color vision is present, with the greatest sensitivity in the green and blue-green region. The placement of the eyes forward and high on the head suggests an adaptation to looking upward and forward, with considerable binocular ability for judging distance. This may aid in locating breathing holes in ice (Kooyman, 1968), in hauling out on rocks, and in capturing prey (Hobson, 1966).

That vision may not be an essential sense in some species is suggested by statements that blind grey seals successfully feed and pup. Furthermore, the fact that Weddell seals feed in the almost lightless winter of the Antarctic suggests that sound may have increased importance. It is possible that the presence of a high level of phosphorescence allows Weddell seals to communicate and locate prey visually (Kooyman, 1968). Ponting (in Kooyman, 1968), while watching Weddell seals during the winter night at McMurdo Sound, stated, "a seal emerged, its beautiful head all blazing with phosphorescence." It seems reasonable that any available light is utilized by the Weddell seal for orientation and hunting (Kooyman, 1968), especially in clear water. Kooyman (1975) has shown that Weddell seals dive deeper, more frequently, and longer during the day than at night, again suggesting the importance of vision. Kooyman (1968) suggested that seals can see as deep as 1,000 m using both phosphorescence and ambient light. Lythgoe and Dartnell (1970) suggested that the rhodopsins of the elephant seal eye are adapted to the bioluminescence of prey squid (see also Jamieson and Fisher, 1972). Also,

Schusterman (1967) characterized the California sea lion as primarily a visual animal.

A variety of studies have demonstrated good vision in pinnipeds (Schusterman, 1965, 1967, 1968; Schusterman and Balliet, 1970, 1971; Schusterman and Feinstein, 1965; Schusterman and Thomas, 1966). California sea lions, Steller sea lions, and harbor seals are capable of discriminating a size-difference ratio as small as 1.06:1 under water, an ability similar to that of several species of monkey. Under dim illumination the seal's visual acuity is superior to man's, and visual shape and spacing discrimination in seals is highly efficient. It has been hypothesized that seals produce clicks when visual cues are scarce or unavailable, but that they are normally dependent on the visual sense under water.

Schusterman and Thomas (1966) suggested that the visual perceptual organization of seals may be quite different from that of terrestrial animals because seals perform many tasks while upside down or on their sides. A variety of acuity tests suggest that the eye has excellent resolution both in air and in water under lighted conditions, but is much better in water under low-light conditions. Some apparent species differences in reaction to objects (e.g., man) on land may be due to variable selective attention factors rather than to visual acuity *per se* (Schusterman and Thomas, 1966).

Audition

Hearing and sound production both under water and in air are well developed. Acoustic signals are varied in both media, but are still poorly known under water.

Audiograms have been made in both air and water for several species and are summarized in Fig. 1. A recent in-air audiogram of the California sea lion (Schusterman, 1974) does not differ fundamentally from the audiogram made from an evoked potential study (Bullock et al., 1971). Not included in Fig. 1 is the underwater hearing

curve of the ringed seal (Terhune and Ronald, 1975). Seals have good hearing under water and raised thresholds in air, although the grey seal seems to be an exception at 2 to 4 kHz. Where there are lowered thresholds they are variable from 2 to 4 kHz and 15 to 30 kHz. The lowest thresholds in the high frequencies are near or centered at 20 to 35 kHz for the grey seal, near 15 kHz for the harp seal, and between 12 and 40 kHz for the harbor seal. The ear seems best adapted to hearing in water, with some accommodation for in-air hearing. Interestingly enough, much of the prime energy in many vocalizations is from 0.5 to 4 kHz (in the range of best aerial hearing), except for the clicklike sounds discussed below, which have their main energy in the second low-threshold area of the

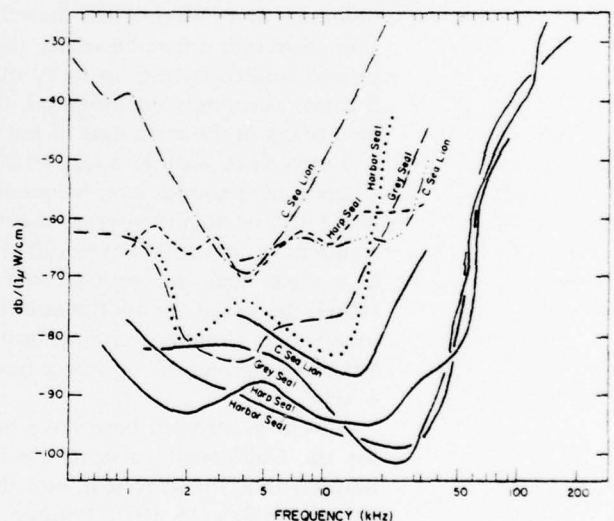


Fig. 1. Underwater (solid lines) and in-air (other lines) audiograms of some seals: harp seal in air (from Terhune and Ronald, 1971), under water (from Terhune and Ronald, 1972); harbor seal in air and under water (from Møhl, 1968a, 1968b); California sea lion in air (from Bullock et al., 1971; Gentry, 1966), under water (from Schusterman et al., 1972); grey seal in air and under water (from Ridgway, 1973).

audiograms at the higher frequencies. Other detailed comparisons of audiograms may be found in Schusterman (1974) and Terhune and Ronald (1975).

One must ask why there is a second area of decreased thresholds at high frequencies. Although it is not our intention to review the problem of echolocation in seals, a few observations should be made. Poulter (1963) reported that seals echolocate using clicks. Others (Evans and Haugen, 1963; Schusterman, 1974) could not find any evidence for echolocation. Certainly, on the basis of limited evidence, seals do not appear to produce clicks as frequently as do odontocetes. To clarify one problem, we need a definition of a click. Winn and Perkins (1976) defined it as a sound of less than 5 msec in duration, although it may be useful to include some pulsed sounds lasting up to 20 msec. Although it is not absolutely documented, there seems to be a break in the durations of pulsed sounds up to a next class, with durations of 50 to 200 msec. These longer sounds have frequencies only up to 5 to 7 kHz normally, whereas short "clicks" have frequencies up to 30 to over 100 kHz. Therefore, it is clear that the sounds that Schusterman (1967) discussed are not the ones expected to be involved in a refined echolocation system. They are too long and of too low a frequency (up to 4 kHz).

Clicks as defined here have been described for the California sea lion, the harp seal, the hooded seal, the grey seal, and the harbor seal (Mohl and Ronald, 1970; Poulter, 1963; Schevill et al., 1963; Schneider, 1974; Schusterman et al., 1970; Terhune and Ronald, 1973). Schevill et al. (1963) pointed out that seal clicks were much less intense than odontocete clicks, suggesting that their usefulness at a distance must be limited. Much of the equipment used to record clicks has been inadequate for resolving amplitudes at various high frequencies; in fact, there is much distortion (Diercks et al., 1973), and the great variability in the results of physical analyses

of the sounds is yet to be adequately explained. Watkins (1973) discussed this problem in detail.

Seals can localize sounds under water as well as or better than can the harbor porpoise (Table 1) (Gentry, 1967; Møhl, 1964, 1967, 1968a, 1968b.) Localization is improved at higher frequencies, but recently Moore (1975) showed that this is not true for the California sea lion. The harbor seal could detect an average Weber fraction of 0.013 for frequencies of 1 to 60 kHz, but above that, frequency discrimination was lost (Møhl, 1967, 1968b). The minimum audible angle perception for click trains was $9^\circ \pm 4^\circ$ under water and $3^\circ \pm 4^\circ$ in air for the harbor seal (Terhune, 1974).

Touch

The tactile sense is well developed in seals, largely because of the presence of vibrissae around the mouth. These vibrissae are highly developed and have complicated innervations (Cajal, 1952; Ling, 1966; Scheffer, 1962; Stephens et al., 1971). Poulter (1972) suggested that vibrissae are an acoustic sensor and that they respond to low-amplitude high-frequency signals. However, knowledge of the functions of vibrissae of terrestrial animals argues against this hypothesis. Dykes (1972) stated that vibrissae are adapted to discriminate texture and shape of objects within the immediate proximity of the animal's face. Fibers could respond to frequencies up to 500 Hz; a few fibers could respond above that and once even above 1 kHz, where the amplitude had to be increased beyond the usual biological reality. At 20 Hz vibrissae are not sensitive enough to respond to the loudest biological sound ever recorded, namely that of the blue whale (Dykes, 1972).

Chemoreception

Little is known about the senses of taste and smell in seals (King, 1964). Taste buds, although present, are scarce, and a small olfactory bulb exists in the brain. Taste, at least, may be utilized

Table 1
An overview of the reproductive social organization and related events of living seals.

Family and species	Reproductive* social organization	Reproductive habitat	Harem herding	Territoriality	Copulation habitat and time	Where young born	Nursing times and weaning time
Otariidae Sea lions: 5 species	Polygynous.	Intertidal zone and each side of it in water and on land. Sandy and smooth rocky beaches.	No. Only estrous females gregarious.	Male topographic territories. More rigid on rocky than on sandy terrain. C.S.L.	On land and in water. S.S.L.: 6-16 days post partum; S.Am. S.L.: few days post partum.	On beaches, 2 hours to 2 days after arrival.	S.S.L.: go to sea, every 3 days spend one day at sea, weaning about a year or more. C.S.L.: wean at 3-4 months. S.Am.S.L.: wean at 5-6 months. A.S.L.: wean at 3-4 months.
Fur seal: 8 species	Polygynous.	On land; rocky rugged habitats.	Yes. Strong herding but not absolute. Females not as gregarious as above. Herding weaker in S.A.F.S.	Strong male topographic territories.	On land. N.F.S.: 4-7 days post partum. S.A.F.S.: 6 days post partum. S.Am. F.S.: several days post partum.	On beaches shortly after arrival.	N.F.S.: leave 5-10 days post partum for 7-10 day periods, return for 2 days of nursing. Wean at 3-4 months. N.Z.F.S.: wean at 6 months. Wean at 16 or more months.
Odobenidae Walrus	Polygynous.	On ice and in water.	No.	Female nursing herds. Separate male and young herds.	In water. Pehaps after weaning.		Wean at 16 or more months.
Phocidae Northern elephant seal	Polygynous.	On land.	Yes. Very weak herding.	Male territories.	On land. Several days before weaning.		On land. Wean at 4-6 weeks.
Southern elephant seal	Polygynous.	On land.	Yes. Very weak herding.	Male territories.	On land. Suggested first copulation in water. 2 weeks post partum.		On land. Wean at about 3 weeks.
Grey seal	Polygynous and monogamous depending on population.		Harems but no herding.	Male territories.	On land, ice, occasionally in water.	On land.	On land, less common in water. Wean at about 3 weeks.

Family and species	Reproductive* social organization	Reproductive habitat	Harem herding	Territoriality	Copulation habitat and time	Where young born	Nursing times and weaning time
Hooded seal	Family units of larger male, female, and pup.	On ice and in water.	No.	Family territories.	In water. 12-14 days post partum.	On ice.	On ice. Wean at 10-12 days.
Bearded seal	Monogamous, essentially nongregarious.		No.		In water; perhaps a year after birth of pup.	On ice floes.	On ice and probably later in water. Wean at several weeks.
Harbor seal	Monogamous, essentially nongregarious.	In water, intertidal rocks, on ice; population differences.	No.		In water.	Edge of shore, on ice in some populations.	Enter water after birth. Wean at 3 weeks; one population weans at 3 weeks on ice.
Ringed seal Related Caspian and Baikal seals			No.		In water.	In ice or snow lairs; landfast ice only.	In lair, female goes into water periodically. Ringed weans at 2 months. Caspian weans at 4-5 weeks.
Harp seal	Monogamous.	On ice and in water.	No.	Perhaps no strict underwater territories.	Mostly in water; at weaning.	In large female aggregations on ice.	On ice. Wean at 2-4 weeks.
Banded seal	Presumed monogamous.	In water.	No.		In water, 1-2 months post weaning.	On ice.	On ice. Wean at 6 weeks.

Table 1 (continued)
An overview of the reproductive social organization and related events of living seals.

Family and species	Reproductive* social organization	Reproductive habitat	Harem herding	Territoriality	Copulation habitat and time	Where young born	Nursing times and weaning time
Weddell seal	Polygynous	On ice and in water.	No. Groups of females up on ice.	Male under-water territories.	In water; end of weaning.	On ice.	On ice; wean at 6 weeks.
Crabeater seal	Perhaps non-gregarious (gregarious nonbreeding).	On ice.	No.		Presumed in water; end of weaning.	Presumed on ice.	Presumed on ice. Wean at 2-5 weeks.
Leopard seal	Apparently solitary.	On ice.	No.		In water; end of weaning.		Wean possibly at 2 months.
Ross seal	Apparently solitary.	On ice.	No.		Presumed in water; end of weaning.		
Monk seals, 2 living species	Small groups; not polygynous.	On beaches, and now on sand spits.			Presumed in water; end of weaning.	On land.	On beaches. Wean at about 5-6 weeks.

NOTE: Some details of variation due to habitat, subspecies, ages, etc. are not shown. See text for scientific names. C.S.L. = California sea lion; S.S.L. = Steller sea lion; S.A.F.S. = South African fur seal; N.F.S. = northern fur seal; S.Am.F.S. = South American fur seal; N.Z.F.S. = New Zealand fur seal; S.Am. S.L. = South American sea lion; A.S.L. = Australian sea lion.

*The documentation for presumed monogamy is poor for some species of phocids.

in the final selection of food and, perhaps, minimally in communication. Final identification of pups by a mother may involve odors; and northern fur seal, California sea lion, ringed seal males, and probably other species have strong odors that could communicate information about sexual status and even be used in individual recognition. No exocrine glands have been described for seals. Apparently the scent of man is detected by seals on land, and it has been suggested that a seal can smell the presence of a trainer not in view (Evans and Bastian, 1969). It is presumed that the nares are closed under water, so that olfaction cannot be used. The involvement of chemical cues in mother-pup recognition is discussed in a later section.

SOCIAL ORGANIZATION

Seals generally have short, well-defined breeding seasons on traditional grounds and are dispersed to varying extents at other times of the year. Insofar as social systems are concerned, of the 32 species of seals, 14 are social (usually haremlike) breeding otarids (sea lion, fur seals, and walrus). Walrus, although polygamous, do not have harems, but nursery herds, separate from males and nonparturient females, are formed (Burns, 1970). Mating in the polygynous otarids occurs shortly after parturition. Of the 18 phocid seals, two elephant seal species and some grey seal populations are also social haremlike breeders, while most others maintain loose aggregations or are more solitary and only come together briefly to mate.

Male Weddell seals maintain an underwater territory below a breathing hole and presumably an above-water territory near perennial cracks in the ice in the vicinity of an aggregation of territorial females with pups (Cline et al., 1971; Mansfield, 1958; Isenmann, 1970). They are polygynous, with mating taking place in the water. Most of the other phocids are less social and usually monogamous; they mate under water but

haul out frequently to form small or large aggregations. Mating occurs at weaning. For instance, the ringed seal female and pup have snow or ice lairs on landfast ice. Harp seal females haul out on ice in large aggregations to give birth; the males are in the water in groups but start to come up on the ice three to four days after parturition, before mating, probably monogamously, in the water at weaning time (Sergeant, pers. comm., and 1963; Terhune, pers. comm.). The bearded seal pups on ice floes. Hooded seals mate on land and organize into family units of a large male, a female, and a pup (King, 1964) and are much more spatially separated than harp seals. Leopard seals appear more solitary, as is probably the case with the Ross seal (King, 1964); whereas crabeater seals seem partially gregarious, although little is known about pupping. What little is known of Hawaiian monk seals indicates that loose aggregations of females with pups are found and that sometimes a male is with them, thus suggesting some sort of pairing (Rice, 1964; Wirtz, 1968; Kenyon and Rice, 1959). Harbor seals mate monogamously in the water and are essentially nongregarious in the mating season. The general social organization and related behavior are summarized in Table 1.

In the polygynous otarids, the fur seals, except for the African fur seal, exhibit the strongest herding behavior. The northern fur seal is the most active herder; the remaining fur seals are not quite as active. The more sexually dimorphic, larger sea lions and the similar African fur seal (Rand, 1967) show no, or very weak, herding behavior (Miller, 1974). In phocids the highly sexually dimorphic elephant seals weakly herd females, and the grey seals show almost no herding behavior. Miller (1974) has related weak herding behavior with exaggerated sexual dimorphism (large male size), need for less locomotion, and habitat differences. It is easier to herd on rocky rugged terrain. Perhaps herding is relatively ineffective for reproductive success but conserves energy when landmarks are abundant.

The polygynous, harem-forming seals exhibit numerous adaptive variations in their social organization. While northern elephant seal females stay with their pups during a thirty-day nursing period, fur seal mothers leave their pups for six-to-seven-day periods of feeding at sea. Thus, fur seal pups can fast for long periods; while in the elephant seal the pups must feed almost every day, but the cows can fast for long periods. Communication for reunification after long and distant separation must be more evolved in fur seals. Steller sea lion females leave their pups and go to sea for a few hours to a few days, then return to nurse for two days (average cycle three days) (Gentry, 1970).

Other social systems exist in addition to the terrestrial harem organization of the elephant seals and fur seals. In Weddell seals, different phases of breeding are consummated in two media: the females aggregate and the pups are born along perennial cracks in fast ice, while polygynous males defend breathing holes against subordinate males and mate in the water. Less-dominant males and nonreproductive females are distant from the rookery (Lindsey, 1937). This situation, in addition to freeing space for parturient females that would normally be occupied by males, minimizes pup disturbances caused by intermale conflict, so characteristic of restricted breeding grounds. Furthermore, acoustic and postural displays are required by Weddell seal males when approached by other males under water.

In Steller sea lions, on the other hand, first the males occupy terrestrial, aquatic, and semiaquatic territories. Then the females arrive and establish favorite spots in aggregations, particularly in the semiaquatic areas (Gentry, 1970; Sandegren, 1970), so that several females are within one male's territory. The males' territorial boundaries are well defined by ritualized threats, fighting, and geographic demarcations (Gentry, 1970). The females tend to move between two or three favored resting sites rather than randomly

across the reproductive area, but they do cross some male territories. In addition, herding bulls sometimes try to prevent cows from leaving territories (Orr and Poulter, 1967), but the response is weak when compared to that of strongly herding species. Herding is directed exclusively toward cows with young pups or estrous cows, and may be initiated by the cow. The females form dominance hierarchies, in which the more aggressive secure and defend the more favorable pupping sites, have greater nursing vigor, and, through activation behavior, aid in the development of the pup.

Peterson (1965) stated that "fur seal harems are aggregations of otherwise solitary individuals." In this situation, successful breeding can result if aggression due to crowding is reduced. In the northern fur seal, this is achieved through strict territoriality, harem maintenance, and agonistic signaling. The timing of social events is briefly: Northern fur seal bulls come ashore early in the season and establish territories near the water's edge. As the season progresses, areas more inland become territorialized, and the size of those territories already established is forcibly reduced by crowding. The harem bulls usually maintain positions throughout the season and repulse nonterritorial bulls. The majority of the pregnant females return after the males establish territories. The females, like the males, normally return to the same location every year. During the next eight days, the females pup, come into estrus, and mate. The females then return to the sea for food, returning to the rookery every seven to nine days to nurse. The breakup of the breeding assembly is caused by the females' desertion and by the waning of territoriality in the male. Except for this breeding period from May to August, Northern fur seals are at sea.

In the elephant seals, several factors affect communication: exaggerated male size, leading to poor locomotion; increased female gregariousness; increased female aggression during the breeding season, due to the males' defense of

their proximal position near the females; and maternal protection of pups. Because of these factors, pressures develop to restrict violence, to allow effective territorial behavior, and to limit the need for terrestrial locomotion.

Territorial behavior is almost ubiquitous in seals, although in some phocids where fixed geographic cues are lacking, only individual distances are maintained. In the polygamous forms, a territory may be as small as 10 X 10 m; whereas in the ringed seals (Olds, 1950), family units space out at least 50 m or more. In phocids, most females with pups defend their territories, as the males of most species probably do during the mating season. The male territories are frequently in the water, but it should be emphasized that little is known, and individual spacing without reference to an area may be the rule. A few species are solitary to a certain extent, although haul-out areas are reported, and normally they are spaced out individually (leopard seal: Marlow, 1967; Gwynn, 1953; probably Ross seal: Laws, 1964). Related to this is the fact that males are larger than the females. Males of many species have secondary sexual devices that, in some cases, may amplify sounds. They consist of nasal sacs in elephant seals and in hooded seals, large neck "shields" in fur seals, and an elongated nose in grey seals. Pharyngeal pouches occur in the walrus, and similar, less well developed devices have been suggested for ribbon seal, northern sea lion, bearded seal, ringed seal, and harbor seal (Schevill et al., 1966). Some males, such as the harp seal, may be nonterritorial (Sergeant, pers. comm.).

The development of communication systems that enhance adaptation of individuals result in social organizations in seals that are critical for at least three functional needs: the maintenance of close proximity between mother and young during the suckling stage and their reunification after the mother has gone to sea to feed (particularly for otarids); the maintenance of the

harem (or social pair in some species) by male-to-male agonistic signals and by the herding of females; and courtship and copulatory signaling. After the seals finish reproductive activities and leave for sea to feed for the remainder of the year, they are generally more solitary, and complex signaling systems are not known, although in some seals pairs or small groups are maintained.

The interaction of the above communication needs is intimately tied to pup survival. This is true for the harem- and social-breeding species, which include all otarids and a few phocids. Much of the pup mortality in some species is socially induced (Le Boeuf, 1972). Thus, although communication reduces mortality, it is not efficient enough to prevent significant mortality. For instance, Le Boeuf (1972) gave four prime causes of death of northern elephant seal pups, each of which involves a breakdown in communication (social disorganization): mother-pup separation without reunion, failure of some females to nurse alien pups, female aggression toward alien pups, and bulls trampling young pups. These same problems occur with other social pinnipeds, e.g., grey seal (Coulson and Hickling, 1964), monk seal (Wirtz, 1968), northern fur seal (Anonymous, 1971). Less is known about ice-breeding species.

In the polygynous species, the communicative system must deal with several factors, including increased male size and aggression, female gregariousness, female defense of pups, and exclusion of nonreproductive individuals. Communication must therefore function to restrict violence, maintain spatial relationships, and limit the need for terrestrial locomotion so that the individual can function efficiently.

COURTSHIP AND MATING SIGNALS

The structure of the mating system develops out of a need for competing males to have access to females. It is represented by two situations:

that in which a male has access to many females (polygyny), and that in which only one male has access to one female (monogamy). In many species mating occurs exclusively in water, in others only on land, and in some species in both environments.

As a consequence of a structured social organization, and perhaps because they are accessible for study, seals breeding in environments restricted by breathing holes (on ice) or by topography (on land) are reported to have complex signaling and breeding systems. A variety of signals, including odor, color, posture, taste, and sound, are involved in courtship behavior.

Courtship and mating occur in the water for such species as the Weddell seal (Cline et al., 1971), harbor seal (Venables and Venables, 1957), harp seal (Silvertsen, 1941), and leopard seal (Marlow, 1967). Although complete behavioral analyses are lacking, we do know that mating is preceded by various displays. Male Weddell seals call actively beneath the ice. This may induce nursing females above the ice to peer down the breathing hole (Kaufman, in press), and the females' behavior may have communicative function as well.

Courtship is poorly known in the harbor seal since it occurs offshore between individuals that are not sexually dimorphic. Courtship signals are apparently produced while the seals are swimming, blowing bubbles, and vocalizing (Venables and Venables, 1957). In the harp seal and the Weddell seal, the male coaxes the female into the water with locomotory and acoustic displays. Female grey seals may solicit copulation by nuzzling the male (James, pers. comm.). Information on phocid courtship and copulatory behavior is lacking because they occur in water, where few observations have been made.

Males assess estrus by olfactory investigation. Territorial male New Zealand fur seals sniff rocks used by females as well as the females themselves (Miller, 1974). Miller stated that assessment of

the female reproductive state by chemical cues may be absent in northern fur seals, but it is the rule in otarids. Scent glands are unknown in seals. What role the musky odor of male California sea lions and northern fur seals plays is unknown (Peterson and Bartholomew, 1967). Male ringed seals (Kenyon, 1962) and harp seals exude strong odors. Perhaps this odor is used in territorial marking.

Otarids, excluding the walrus, normally mate on land (Sandegren, 1970; Gentry, 1970), as do two socially similar phocids, the elephant seal and the grey seal, which occasionally also mate at sea.

Otarid males investigate the anogenital area of the female before copulation. Their interest may be increased by the swollen red vulva, which sometimes induces them to lick the region (Bartholomew, 1953; Bartholomew and Hoel, 1953; Gentry, 1970).

The female otarid often solicits copulation in a much more active and elaborate manner than do female phocids. Most prominent are the exaggerated walk of the estrous display in female northern fur seals (Peterson, 1968) and the solicitous precopulatory display of female Steller sea lions, which may be essential to induce the male to mount (Gentry, 1970; Sandegren, 1970). Signaling in the fur seal (Peterson, 1965) during "estrous" displays consists of nose and head rubbing and nipping the bull's neck and mandible. The females become less and less aggressive. The vibrissae are usually erect. The male produces the extended low roar, while the female sometimes hisses. When not in estrus the female gives the "evasive" display typical of all nonestrous male-female encounters. It is a combination of avoidance and threat, with the vibrissae erect and the neck arched. The bull attempts to keep the female in his territory while threatening vocally. A female may face the bull and grip his mandible or the underside of his neck in her teeth. This seems to limit his nipping

at her back since she is firmly locked to him and moves with him during attempted lunges. Sometimes the female does not establish a firm grip and simply counters the bull's lunges at her with aggressive, open-mouthed threats of her own.

If the female proves to be sexually unreceptive, the "whicker" and the extended low roar are used in alternation by the male. If aggressive threatening and physical blocking are not sufficient to stop an escaping female, a bull can forcibly bend her over until he can grasp the skin of her back in his teeth. Then he may lift her bodily and throw her into his territory.

When ready to accept mounting, a female permits the bull to nuzzle her perineum and rub his whiskers along her back, which is arched upward, while the hind flippers are spread. Sometimes a female seems to be suddenly intolerant of a bull and breaks into evasive display. A female's estrous display always induces a bull to mount.

Northern elephant seal bulls sometimes mate immediately after a successful agonistic behavioral interaction (Bartholomew, 1952; James, 1970) and may be only secondarily stimulated by the presence of females. James (1970) hypothesized that this is a result of general arousal or, more probably, the disinhibitory effect of stimulation provided by an intruder on a beach master habituated to female presence.

Precopulatory displays by the New Zealand fur seal are much less frequent than those of sea lions (Miller, 1974). Miller states that the tactile components are much less developed than for sea lions. Token female resistance and passivity carry stimulus values to male seals.

Copulatory behavior itself is quite stereotyped. Basically the male positions himself behind and on top of the female, thus controlling her with his weight and/or foreflippers. The posture in some species changes so that the male is on the female's side (grey seal: Hewer, 1957). Rubbing of partners just before and during copulation occurs more often in the thigmotactic sea

lions and South African fur seal than in other fur seals (Miller, 1974).

During aquatic mating (Weddell seal: Cline et al., 1971; harbor seal: Venables and Venables, 1957; Bishop, 1967; leopard seal: Marlow, 1967), the male grasps the axillary area of the female with both flippers. In terrestrial mating of other species one foreflipper is positioned over the female dorsal, and the male's weight is both on the female and on the substrate, so that the male is partially on his side, though during the early stages, the male may be on top briefly (Carrick et al., 1962; Schneider, pers. obs.). Neck grasping by the male induces the female to be more passive. She may bite his neck, possibly encouraging him to dismount at the end of mating.

Terhune (pers. comm.) has seen harp seal cows with cuts and scratches on various anterior parts of the body, some of which were thin lines one to six inches long running along the shoulder anterior to posterior. They could have been made by the nails of the foreflippers and by biting the female's neck if the male had mounted from behind under water.

Herding of females by males to maintain harems is not generally very effective in pinnipeds. Sea lions, the South African fur seal, and the northern elephant seal are less-successful herders than the smaller fur seals, perhaps because their large size limits their locomotion. In all cases, the tendency of the females to stay in one place is as important as efficient herding to maintaining a harem. As a result, Miller (1974) suggested that the most important function of herding behavior is to communicate criteria for normal males in a group of animals where mate choice is apparently lacking. In a sense, it may be functional, like courtship activities.

MOTHER-PUP SIGNALS

Just prior to parturition, the females establish a territory. In otarids, the northern elephant seal, and the Weddell seal (Kaufman, 1975), the

females may aggressively clear areas. Though the duration of nursing varies among the different species, there are several advantages to maternal maintenance of territory and establishment of a consistent place for suckling. First, adoption by violence is discouraged in stable nursing situations (Le Boeuf et al., 1972), although exceptions to this rule exist (Burns et al., 1972; Marlow, 1972). Second, the female's territory provides a defending area in which disturbance of the pup by other females, and of the mother by males and females, is minimized. Third, female territoriality lays the groundwork for precision in geographic reunification of nursing otarid pairs.

In otarids, the mothers leave the young to go to sea, presumably to feed, and then return periodically to nurse their pups. Northern fur seals, for example, leave five to ten days post partum for periods of seven to ten days and return for two days of nursing (Peterson, 1965). Pups generally remain near the birth site, and the mother returns to shore near the site; thus, geography and spatial memory play an initial role in reunification. Successful reunification also depends on the development of signals—acoustic, visual, olfactory, and tactile—for mutual recognition between the mother and the pup.

Acoustic signaling in some species may start when the female directs calls at the anogenital region just before the birth of the pup. This behavior may be the beginning of the establishment of the mother-pup bond. In otarids, mutual vocalization starts immediately after birth (for example, the northern fur seal: Peterson, 1965). Calls made by nursing pairs have been termed mother attraction and pup attraction (Table 2). Though both types are reported for most pinnipeds, the grey seal and the harbor seal use only the mother-attraction call. This call is vocalized by young pups when distressed, when being abused physically (in elephant seals), or when apparently hungry. Pup-attraction calls, emitted by the mother, seem to contain more specific

meanings and are used only during reunification or activation (Sandegren, 1970). The northern elephant seal mother starts calling as soon as she comes ashore. This sound is easily heard above all the other sounds in the colony (Bartholomew and Collias, 1962). Maternal calls are individually identifiable, but pup recognition of the call may take varying amounts of time to learn, from three days, in the northern sea lion (Sandegren, 1970), to two months, in Hooker's sea lion (Stirling, 1972). Rand (1967) noted learning in the South African fur seal, in which pups initially respond to pup-attraction calls of all females, only later answering to the call of a specific cow. In the northern fur seal, pup-attraction calls cease when the seals are reunified, whether or not suckling follows. Several authors (Wilson, 1973a; Fogden, 1971; Evans and Bastian, 1969) concluded that harbor seals, which nurse primarily in the water, attract pups through smacking the water, circling and nuzzling the pup, or whole-body contact. The pup does not recognize the mother, and pups initiate suckling by calling and nuzzling on approach. Terhune (pers. comm.) stated that in the harp seal only the pups call. As many vocalizing pups are rejected as are accepted after being sniffed—another instance that suggests that odor is the final cue for identification.

Olfactory and tactile signals may well be used in final identification when the phocid mother approaches the pup (Fig. 2). With one exception, there have been no experimental studies on mother-pup recognition signals. In a series of preliminary experiments, Kaufman (in press) determined that odor was important in Weddell seal reunification. In one experiment, the skin of a dead pup was attached to a live pup. The live pup was accepted by the mother of the pup that had died, from which the skin had been taken. Kenyon and Rice (1959) related an incident in which a Hawaiian monk seal mother, separated from her pup, heard the cry of an isolated, nearby pup and rapidly crawled to it. She sniffed

Table 2
Use and description of pinniped vocalizations.

Vocalization	Use	Description
Northern fur seal (Peterson, 1965)		
Male trumpeted roar	Territorial	Loud, prolonged call; variable in pitch, rate, and volume; 5-sec burst with rising pitch; rapid repetition when intensity is high; volume varies with intensity.
Low roar (male)	Immediate	Short, loud, not pulsed; intergrades with trumpeted roar; duration 1 or 2 sec.
Whicker (male)	Mild threat	Resembles clicking; little variability in pitch or volume; constant repetition rate, but slower toward end of series.
Boundary puffing (male)	Territorial boundary display	Harsh, panting; a sharp exhalation repeated several times in rapid succession; diminishing volume.
Whine (male)	Submission	Loud, high-pitched squeal; duration 3-5 sec.
Open mouth threat (female)	Threat	Hiss.
New Zealand fur seal (Miller, 1971; Stirling and Warneke, 1971)		
Trumpeted roaring (male full threat call)	Threat; boundary display	Pulsed, growllike sound, followed by screamlike portion; mean duration 1.4 sec.
Male low-intensity threat	Threat	Pulsed growllike sound; major energy below 1.7 kHz.
Male moan	Not clear; probably agonistic	Cowlike moo; duration 2 sec.; major energy <1,000 Hz; side bands present.
Male guttural challenge	Threat; territorial	Low-pitched growl followed by single pugg.
Male barking	Sexual interest; territorial	Repeated high-pitched call.
Jaw clapping	Agonistic	"Fwapp."
Snort	Weak Threat	Snort.
Submissive call (male and female)	Submission	Modulated high-pitched call; 2-4 kHz; duration $\approx 1\frac{1}{2}$ sec.
Pup attraction (female)	To attract pup	(1) High-pitched whine, similar to horse whinny; 1.5 kHz. (2) Lower-pitched monotonic moan; 0.15 kHz; pulsed.
Female attraction (by pup)	To attract female	High-pitched call; first section has low fundamental frequency (as low as 2.5 kHz); second section has higher frequency (1.6 kHz); duration to 15 sec; first section always 0.5 sec.
Chung	Threat	
Open-mouth threat (female)	Threat	
Bleat and bawl (pup)	Female attraction	
Chirp	Inquiry	Downward-swept frequency varying between 30 and 1 kHz, often repeated in series.
Low pulses	Threat	Less than 200 Hz, duration 0.5-1.0 sec.

Table 2 (continued)

Vocalization	Use	Description
Hawaiian monk seal (Kenyon and Rice, 1959)		
Soft bubbling sound	Alarm	Sounds like "bgg-bgg-bgg-bgg"; originates deep in throat.
Grunting bawl (female)	Threat	Expelled air forms snort, snort bellow, or "mrrough" sound; similar to that made by <i>Eumetopias jubata</i> .
Bleat (pup)	Female attraction	Similar to adult bellow; sounds like "mwaa-mwaa-mwaa."
Grunting bawl (pup)	Threat	Diminutive version of adult grunting bawl; "aaah" or "gaah."
Growl or moan (female)	Pup attraction	Hoarse, throaty.
Harbor seal (Scheffer and Slipp, 1944; Evans, 1967)		
Various sounds	Not known	Snort, squall, bawl, throaty grunt, doglike bark.
Flipper slapping	Alarm; pup attraction	Flipper slaps water surface during diving.
Pup calls	Mother attraction; distress	Sounds like "maa" or "kroo-roo-uh"; about 500 Hz.
Bearded seal (Ray, Watkins, and Burns, 1969)		
Male song	Territorial	First section: modulated warble; long, oscillating frequency; may be 1 min in duration. Second section: moan; short, unmodulated frequency. Call starts at about 2,000 cps and ends as low as 200 cps.
Ringed seal (Stirling, 1973)		
Bark	Direct threat	Low-pitched.
Yelp	Probably submissive	High-pitched, sometimes modulated.
Growls	Threat	Low- and high-pitched.
Chirp		Short, descending frequency.
California sea lion (Peterson and Bartholomew, 1969)		
Bark (male)	Aggression; territorial	Duration .2-.3 msec; 3 barks/sec; fundamental 200 Hz; produced almost continuously at height of breeding season.
Female threat	Threat	Bark, squeal, and growl; used with open-mouth threat.
Mother response	Response to pup attraction	Individually varied; similar to bawling.
Pup bark	Play; mild threat; when disturbed	Higher frequency than adult bark; 3-8 barks in succession, pulsed.
Pup attraction (female)	To attract pup	Individually varied; duration 1-2 sec; bawling sound; may be pulsed.
Walrus (Schevill, Watkins, and Ray, 1966)		
Bell	Sexual behavior	1.0-1.5 sec; fundamental 400-1,200 Hz.
Rasps and clicks		

Table 2 (continued)
Use and description of pinniped vocalizations.

Vocalization	Use	Description
Northern elephant seal (Bartholomew and Collias, 1962)		
Clap threat	Threat	Loud, resonant clapping sound with metallic quality, like exhaust noise of a locomotive; frequency <2,500 cps; extremes recorded of bursts of 3-7 pulses at a rate of 15-25/sec with 0.1 sec between bursts, and single claps spaced at 1-sec intervals.
Snort.	Threat	Snort.
Whimper.	Submission	Whimper.
Female threat	Threat	Harsh, deep, belching roar; frequency <700 Hz; pulse rate changes from 100/sec to 50/sec; duration >3 sec.
Pup attraction (female)	To attract pup	High-pitched bark; frequency 500-1,000 Hz; duration 0.2 sec; repetition rate and intervals between barks not constant.
Female attraction (by pup)	To attract female	(1) Long, puppylike yelp; duration 0.3-0.5 sec; repeated several times; ascends to 1,000 Hz; pulsed 80-90/sec. (2) More fluctuations in pitch than type 1; ascends from 100 to 1,000 Hz.
Weddell seal (Kooyman, 1968; Schevill and Watkins, 1965; Watkins and Schevill, 1968)		
Chi-chi-chi	Threat	Series of short-duration pulses; series as long as 42 sec; frequency and repetition rate start high but drop gradually during series.
Trill	Threat; dominance	Descends continuously from 6 kHz to 0.5 kHz in 1.5 sec.
Eeyo	Threat	Frequency stays constant at 3,500 Hz for 2 sec, then changes to 250 Hz.
Teeth clattering	Threat	Jaws open and close rapidly; maximum gape 5 cm.

it several times, left, and continued to search. Odor recognition may also be important in the grey seal (Burton et al., 1975). The subject of mother-pup signals is obviously wide open to experimentation in various species.

The pinniped nursing period is prolonged, particularly in the socially breeding otarids. Steller sea lion may nurse for a year, northern fur seal for three months, and northern elephant seal (a phocid) for about a month. The California sea lion nurses on land for about twenty days and then continues for up to six months in the water. Phocids generally nurse for only three or four weeks.

Sandegren (1970) and Gentry (1970) described interesting female Steller sea lion behavior termed activation, which was used to induce, by aversive conditioning, suckling and other behavior by the pup. The mother lifts and drops the pup. Its response (activation) is intense irritation, shown by fast movements, head shaking, and bleating, which is transformed into a long, loud scream. Soon, merely a movement of the mother evokes the same reaction. Other activating behavior by the mother included nipping, slapping, pressing, stroking with foreflipper, and nose pushing. These actions apparently stimulate activity, locomotion, and movement, result-

ing in nursing and thus encouraging rapid growth (Sandegren, 1970).

AGONISTIC BEHAVIOR

The social land-breeding seals, including otarids and some phocids, have evolved highly stereotyped and ritualized signal systems. These signals may help separate the individuals, as in male territories, or they may act to keep the animals close to one another, as in harems. In some species, the fighting and rushing of males across areas occupied by females and pups cause considerable pup mortality. Thus, the signaling systems must be efficient enough to reduce mortality to a level where the population is maintained; and successful mating must be ensured. Although little is known about the underwater ritualized behavior of many phocids, we do know that some species, at least, perform highly ritualized aquatic displays.

Many of the threat and attraction displays include visual and acoustic elements; at times, the tactile and olfactory senses are involved as well. Acoustic-visual complexes change with motivation. In ritualized fighting behavior, body postures and sounds are produced. The vibrissae

are erect, and contact is made. Several authors have noted that "vibrissae contact" in greeting is an agonistic signal (Bonner, 1968; Bonner and Laws, 1964; Orr and Poulter, 1967).

Miller (1971) systematized the communication of threat by territorial male New Zealand fur seals (Fig. 3). First, a territorial male perceives another male approaching at a distance. If his vocal and visual displays do not cause retreat, the territorial male then approaches the other closely. If a retreat still does not occur, the territorial male repeats and elaborates upon the signaling. If no submissive behavior or retreat is demonstrated by the alien male, a fight may result. Although fighting is discouraged, the fact that threat displays occasionally terminate with a fight ensures that the more ritualized visual and acoustic threat signals are reinforced. Descriptions of the territorial behavior of many species of social land-breeding otarids and of a few phocids generally agree with Miller's system based on the New Zealand fur seal (northern elephant seal: Bartholomew, 1952; northern sea lion: Gentry, 1970; grey seal: Schneider, unpublished ms.).

In addition to the ubiquitous open-mouth threat (Fig. 4), males of species that maintain territories have other intense and elaborate inter-male warning calls, sometimes more than one per species (Fig. 5). The warbling song of the bearded seal may be the most elaborate. It is emitted by reproductively active males presumably maintaining below-ice territories, and is unlike the "belch roar" of the northern elephant seal. Physically, the frequency-modulated bursts of the bearded seal's call may be analogous to the pulsed nature of the belch roar. The territorial calls of otarids are of low frequency, pulsed, and normally associated with an elevated posture. Since the first threat calls are produced when the interacting animals are relatively far apart, coupling with a posture must occur within visual range, as in the land-breeding otarids, in



Fig. 2. Final pup identification by mother grey seal, presumably by vibrissal contact information and odor. (Photo by Jack Schneider.)

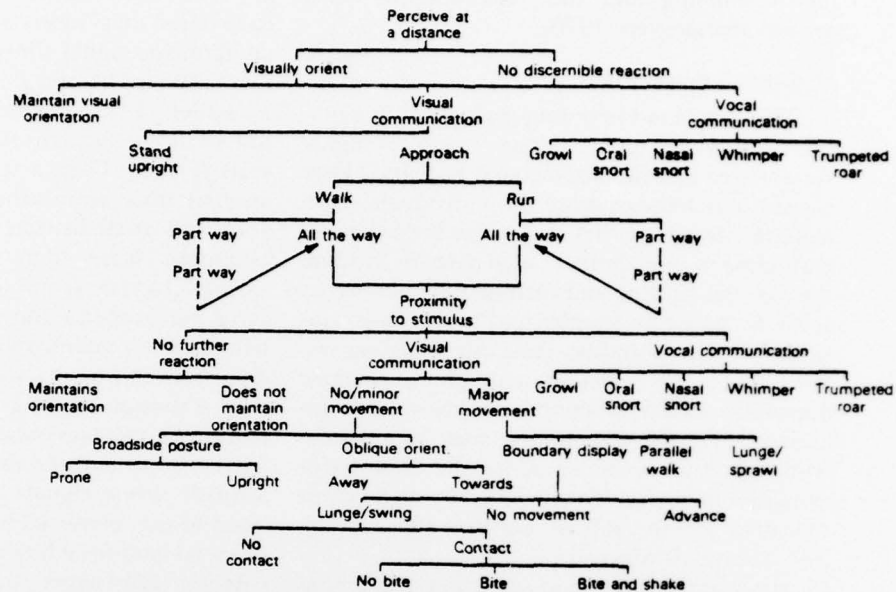


Fig. 3. Communication of threat by territorial males. (From Miller, 1971.)

the northern elephant seal, and under water by the Weddell seal (Ray and DeCamp, 1969; Kaufman, in press). Calling without visual contact stimulates territorial calling in Weddell seals (Watkins and Schevill, 1968) and elephant seals (Bartholomew, 1952). In elephant seals, call amplification conveys dominance; thus large resonating proboscises are positively selected (Bartholomew, 1952). Recent ideas suggest that the call merely identifies the caller and that the proboscis is selected for as a visual stimulus (Le Boeuf and Schusterman, pers. comm.). The barking of dominant male California sea lions restricts the movement and barking by other, smaller males (Schusterman and Dawson, 1968).

Should social relationships of males not be settled by display, fighting occurs. Fighting, perhaps because of seal anatomy, is directed only at certain areas. Biting and height (or getting on top) are fight strategies. During terrestrial com-

bat, biting is directed at the foreflippers, face, neck, and head, though a retreating animal must protect its hind flippers and its posterior dorsal portion from attack. Wounds and scars found on Weddell seals (Kaufman, in press), harbor seals (Naito, 1973), and leopard seals (Marlow, 1967) suggest that the generalized points of aggression are similar in underwater disputes, though the genital region is also a target. In fur seals fighting is ritualized to a point where the animals cease activity if a bite holds (Peterson, 1965). Le Boeuf and Peterson (1969) showed that northern elephant seals actually have a social hierarchy maintained by stereotyped threat displays. Copulation is most frequent by males of the highest status (Le Boeuf, 1974).

Submissive behavior has been described in some otarids (Peterson, 1965; Miller, 1971) and in the elephant seal. The southern elephant seal signals submission by "deflating his proboscis



Fig. 4. Open-mouth threat of a female grey seal toward a mature bull. (Photo by Jack Schneider.)

and backing away, uttering short high-pitched cries" (Carrick et al., 1962). High-pitched whimpers are typical of submissive calls.

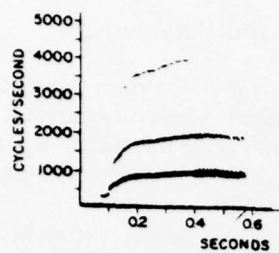
In the northern elephant seal, female aggressive behavior, expressed by brief conflicts and vocalizations, is evoked by intrusions of females, alien pups, yearlings, and any male. If a pup is attacked, it cries and the mother chases and attacks. If her pup is pinned down inadvertently by a male, the female threatens vocally (Bartholomew and Collias, 1962). Much of this signaling serves only to protect the pup. Christenson (1974) has shown that pup survival is related to the aggressiveness of the mother: strong signaling ensures survival, while weakly aggressive mothers frequently lose their pups. With some variations, the social otarids exhibit similar behavior.

Other types of behavior have various signal values. A snort may have universal significance in low-intensity warning. Flipper waving (Schusterman, 1968) is a low-intensity visual warning display that precedes open-mouth threat in grey seals (Schneider, pers. ob.). Flipper waving also occurs in feral harp seals and in captive harp and ringed seals (Terhune, pers. comm.).

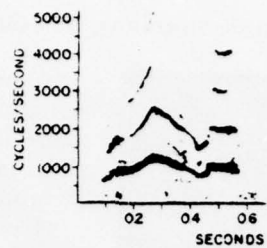
Alert behavior is common. Many of the first signals produced when one animal becomes aware of another serve this function. Underwater clicks may express a mood of alertness or fear (Schusterman, 1967).

Acoustic signals of the social breeders fall into two general groups (northern elephant seal: Bartholomew and Collias, 1962). Threat sounds are loud, harsh, and segmented, whereas attractive calls are less harsh, unsegmented, of variable pitch, and of higher frequency (Fig. 5 and Table 2). Some sounds, such as the male territorial calls, are related to motivational state. For instance, the snort of the northern elephant seal is the lowest-intensity threat sound likely to be the first sound produced in any aggressive situation (Bartholomew and Collias, 1962). It is produced in any position and can cause subordinate males to leave. The clap threat is a signal of incipient attack. It is of higher intensity and is always produced in a stereotyped posture, with the forequarters elevated to the maximum and the inflated proboscis extended into the fully opened mouth. If the intruder does not leave, a fight ensues, usually only when the dominance relation of the bulls has not been established. Subdominant adult males also use these sounds. They are illustrated in Fig. 5, and a summary of the sounds and functions is given in Table 2.

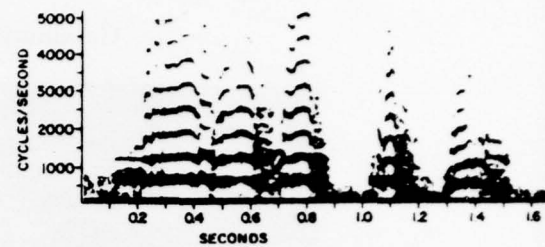
Yearlings produce a hiss and a roar in aggressive situations. The roar is similar to one of the two vocalizations of the female: the belch-roar threat or the high-pitched attraction call, the bark used for maintenance of or finding contact with the pup. The belch-roar threat of the female causes varying responses, depending on the status of the individual being threatened: a yearling immediately retreats; a subordinate female may retreat or reply with similar threat calls; or, if the animals are of equal status, a formalized postural fighting bout may ensue. Bulls are seemingly indifferent to female vocal threats. Bartholomew and Collias (1962) concluded that



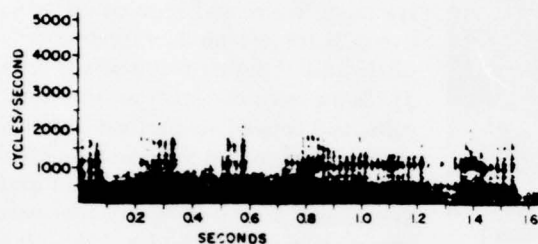
Pup call, Type I.



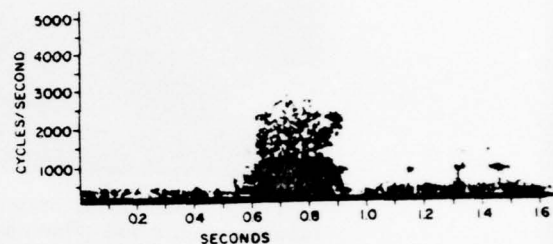
Pup call, Type II.



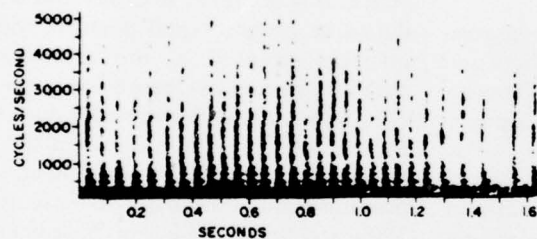
Female attraction call.



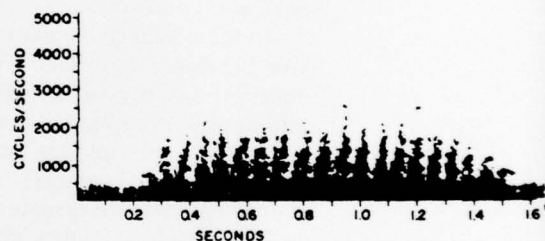
Female belch-roar.



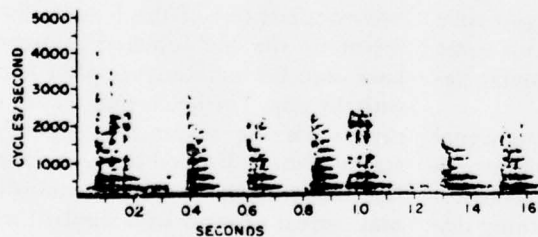
Yearling hiss. The continuous sounds between 200 and 500 cps. represent noise of the surf.



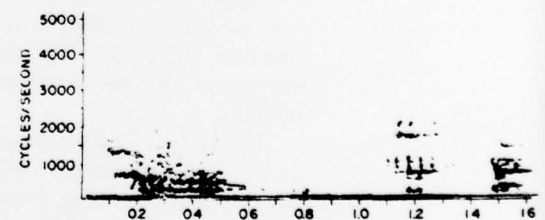
A highly pulsed variant of the yearling belch-roar. This sound was made by a male probably 1½ years old.



Snort of adult male.



Clap-threat of adult male.



Adult male arching into a clap.

Fig. 5. Various sounds of the northern elephant seal. It can be seen that aggressive calls are harsher and pulsed, whereas attractive calls are less harsh and harmonic. (From Bartholomew and Collias, 1962.)

vocal communication is unusually important in the social behavior of the northern elephant seal. They further suggested an ontogeny of the pup protest to the yearling threat, and finally to either the female belch-roar or the mature male clap threat. Other species of social pinnipeds have similar call organization and development.

The threat sounds of the southern elephant seal were found to be quite different from those of the northern elephant seal, two species separated since the Pleistocene (Le Boeuf and Petrionovich, 1974a).

Tactile and olfactory signals are poorly understood. We do know that the erect vibrissae are used in greetings. Bonner (1968) calmed down an aggressive Kerguelen fur seal by stroking its vibrissae with a long stick. There is much evidence that males have strong odors, and it has been suggested that pheromones may act in territorial behavior (northern fur seal: Peterson, 1965; ringed seal: Kenyon, 1962; California sea lion: Peterson and Bartholomew, 1967; New Zealand fur seal: Miller, 1971).

Visual signals are many. They consist of postures, low for submissive behavior, high for aggressive behavior. Open mouths in various threat situations (Fig. 4), with a strikingly colored pink mouth, and the various developments of proboscis and vocal sacs in some adult males are all visual signals.

The existence of dialects in male threat vocalizations of the northern elephant seal has been studied in some detail by Le Boeuf and Petrionovich (1974b). Essentially, they have shown that the call pulse rates of animals from an island that has a few animals is increasing and is correlated with the immigration of animals from another island where animals have a higher pulse rate. The pulse rate of calls from individuals does not vary systematically from year to year. The pulse rates of animals from a rookery with few immigrants has remained relatively constant over a four-year period. Although the functional

significance of pulse rates is unknown, the authors felt that the differences arose as the result of isolation. The differences may well represent the raw material for future speciation.

PLAY

Play may be with objects, self, or other animals, and has been described for the northern elephant seal (Schusterman, 1968; Rasa, 1971), the Steller sea lion (Schusterman, 1968; Farentinos, 1971), the California sea lion (Schusterman, 1968; Peterson and Bartholomew, 1967), the South African fur seal (Rand, 1967), the grey seal (Hewer, 1957; Wilson, 1973b), the Weddell seal (Kaufman, in press), and the harbor seal (Schusterman, 1968; Wilson, 1973a, 1973b). Patterns of play are sex-specific in southern elephant seal and Steller sea lion pups (Rasa, 1971; Gentry, 1974) and frequently include sham fighting, pseudo-copulation, herding (in northern fur seal: Peterson, 1965), and swimming. In the northern fur seal (Bartholomew, 1959), the most frequent type of pup play changes from pseudo-copulation, during the reproductive season, to sham fighting and swimming in autumn. Bartholomew related the frequency of reproductive play to the visual presence of reproducing animals. Peterson (1962) found that sham fighting became more adultlike by fall. Farentinos (1971) made the interesting observation that normally aggressive nursing female Steller sea lions, after leaving their pups, gather and engage in play, which includes mock fighting, wrestling, and synchronous swimming. It appears that play is important to socialization, and thus the ontogeny of communicative behavior (see also Gentry, 1974).

Wilson (1973b), in summarizing play in harbor seals, said that similar dyadic play occurs between mother and pup, small juveniles, adolescents, and adults, commonly as a prelude to coitus, and occasionally outside the mating season. Group and dyadic play occur in the har-

bor seal, but only dyadic play was found in the grey seal. Although the motor patterns found in adult agonistic behavior generally compose play, this was not the case in the harbor seal. The grey seal exhibits a species-specific signal to invite and maintain play not found in the common seal. Wilson concludes that the differences found in the common seal may relate to mating without competition (monogamous).

INTERSPECIFIC COMMUNICATION

Birds often communicate danger to and induce fleeing responses by seals. Bartholomew (1952) describes how gulls first react to a human by mobbing and calling; this in turn alerts the cormorants, which upon the closer approach of man take to the air; and their flight causes many of the elephant seals to take to the water without even determining what the danger is. Gentry (1970) suggested that northern sea lions fled to the water when the alarm cry of the western gull was produced, but the response was not elicited by the cries of other bird species. These relations have not been studied in any detail. Interspecies communication of various seals is known to occur, but will not be covered here.

Summary

Sea cows, sea otters, and pinnipeds each have solved their communicatory needs in different ways. Sea cows are aquatic, and little is known about their communication; whereas sea otters relate more to other otters than to sea cows and pinnipeds. Seals must go onto ice or land to give birth and may be diphylectic. The otarids are polygamous social breeders and usually mate on land. Phocids have some polygamous forms, but are generally monogamous and usually mate under water.

Recent reviews of various aspects of reproduction, social organization, and communication of pinnipeds can be consulted for other references and details not covered here (Peterson,

1968; Caldwell and Caldwell, 1972a, 1972b; Poulter, 1968; Evans and Bastian, 1969; Schusterman, 1968; Ronald and Mansfield, 1976). The more social polygamous species and those that are economically important have been studied the most. Many of the phocids carry out activities in the water and in very rigorous environments, where their accessibility to study is limited.

The pinnipeds exhibit a wide variety of reproductive and social organizations, ranging from solitary to highly gregarious forms. All seals must come up on ice and land to give birth, apparently for thermoregulatory reasons. This fact determines, in some cases, the kind of communication system that is needed. During the remainder of the year seals are generally less gregarious and, in some cases, even solitary.

It is clear that visual, auditory, and to a lesser extent tactile senses are dominant in seals. Vision and hearing are adapted for use under water, where seals spend most of their time, but are adequate on land. This fact correlates with feeding and the presence of predators in water. Colonial seals on land appear to have few predators, but the senses are still adequate in air. Sea lions appear to rely heavily on vision, although sound is useful over much greater distances. Circumstances exist in which the emphasis must shift to the acoustic mode, such as during the antarctic night or in murky waters. Because blind seals frequently appear healthy and are able to pup, we can conclude that the acoustic channel is developed sufficiently to solve their needs in the absence of vision.

Sound and visual posturing are highly developed during mating seasons, and both channels appear useful in maintaining territories, courtship, mating, and mother-young interactions. Broad underwater areas of the arctic and probably the antarctic are completely saturated with mating calls. These "songs" are probably functionally similar to bird song or humpback whale song.

The visual and acoustic senses of seals in water are as well developed as those of primates. Vision seems more important in seals than in the acoustically dominated odontocetes. The placement of the eyes on the side and far back of the head in porpoises leads one to believe that the primary uses of vision may be to maintain coordination of swimming groups and to see to the side where sound is reduced; whereas the forward and upward placement of the eyes in seals adapts them to their particular needs, such as feeding. It is interesting to note that Schevill and Watkins (1971) suggested that the Weddell seal's sounds are directed downward and forward, thus covering an area not within the visual cone; but the projected sounds were not typical echolocation clicks. Although one thinks of sounds as more important in the land-breeding species than in the aquatic mating phocids, Mohl et al. (1975) have tentatively identified sixteen types of sounds produced by the phocid harp seal.

Our knowledge of the chemical senses of pinnipeds is rudimentary at best; but sufficient observations exist to suggest that olfaction is used on land in mother-pup recognition, recognition of musky-smelling males, and recognition of estrous females.

In general, the strategy taken by many pinnipeds, especially the otarids and a few phocids, is to aggregate on barren beaches and to establish social groups. These frequently involve a harem organization. Ritualized acoustic and visual displays have been developed to help maintain the groups, to reduce aggression, to reduce harm to pups, and to ensure continued contact or reunification of mother and pup.

Some species of phocids do not form breeding aggregations; thus there are brief periods of underwater courtship that have only been fleetingly observed in a few species. Mother-young communication is brief, and little is known about the relations between mother and young once pupping areas on ice or land are deserted. In

some species, such as the Weddell and harp seals, a profusion of underwater sound signals have been heard. In fact, courtship may be more highly evolved in the underwater mating phocids. Some phocids also form female aggregations or even family units on ice, and mating more often takes place in water (Table 1).

Territorial signaling is ubiquitous to varying degrees in the social breeders and for those species that have topographic cues under water (e.g., Weddell seal). Under water, many phocid males probably shift to individual spacing, again using acoustic and visual displays. However, the grey seal bull uses sexual activity rather than territorial fighting and boundary displays as a strategy to ensure that he mates with those cows in his area of influence (Anderson et al., 1975).

In general, topographic (returning to and staying in a specific area), acoustic, and olfactory signals of mother and pup are designed to assure reunion in those species where the mother leaves for the sea periodically. Courtship in the polygamous forms is limited, but in some species, such as the northern fur seal, females have estrous displays. Courtship in the supposedly monogamous phocids may be more elaborate under water, but our information is still incomplete. Again, in polygynous species male signaling during reproduction is designed to protect a space, fixed or not, to maintain a harem. Female aggression is primarily designed to maintain spacing before estrus and to protect pups.

Play is sometimes species-, age-, and sex-specific and appears to be important to the proper development of adult signaling systems.

It appears that with the development of polygamy in the otarids and a few phocids, a positive selection for sexual dimorphism exists. The large size of males (three to six times as large as the females in some cases) allows for fasting while holding territories; but more important, sexual dimorphism (vocal sacs, teeth, size) strengthens communication signals. Lim-

ited terrestrial locomotion probably requires emphasis on acoustic displays associated partly with stationary visual displays. The more effective the signals the more females are fertilized; thus, sexual dimorphism is enhanced through positive feedback (see Bartholomew, 1970, for discussion of polygamy). This development in turn requires that signals become highly ritualized and effective, in order to reduce pup mortality from crushing by males. Although some of the more monogamous phocids have limited sexual dimorphism, which is probably useful for territorial maintenance, it does not have such a strong positive selective value.

More experimental research is needed on the roles of sensory inputs in reproductive behavior. The recent expansion of studies on seals should greatly increase our understanding of communication in these animals.

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